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Threshold foraging behavior of baleen whales

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ABSTRACT: We conducted hydroacoustic surveys for capelin *Mallotus villosus* in Witless Bay, Newfoundland, Canada, on 61 days during the summers of 1983 to 1985. On 32 of those days in which capelin surveys were conducted, we observed a total of 129 baleen whales - including 93 humpback *Megaptera novaeangliae*, 31 minke *Balaenoptera acutorostrata* and 5 fin whales *B. physalus*. Although a few whales were observed when capelin schools were scarce, the majority (96 %) of whales were observed when mean daily capelin densities exceeded 5 schools per linear km surveyed (range of means over 3 yr: 0.0 to 14.0 schools km^{-1}). Plots of daily whale abundance (no. h^{-1} surveyed) vs daily capelin school density (mean no. schools km^{-1} surveyed) in each summer revealed that baleen whales have a threshold foraging response to capelin density. Thresholds were estimated using a simple iterative step-function model. Foraging thresholds of baleen whales (7.3, 5.0, and 5.8 schools km^{-1}) varied between years in relation to the overall abundance of capelin schools in the study area during summer (means of 7.2, 3.3, and 5.3 schools km^{-1}, respectively).

INTRODUCTION

Calculations suggest that baleen whales must forage on high density aggregations of prey to meet the metabolic demands associated with their large size (Brodie et al. 1978, Kenney et al. 1986). In support of this, strong temporal and spatial correlations between whale and prey abundance have often been observed (e.g. Whitehead et al. 1980, Paine et al. 1986, Piatt et al. 1989), and extended prey aggregations exploited by fin and humpback whales typically include concentrations with point densities of 10 to 500+ g m^{-3} (Sameoto 1983, Krieger & Wing 1986, Dolphin 1987). There are still few details, however, on the foraging response of baleen whales to variations in the density of their prey. To our knowledge, threshold foraging behavior by baleen whales has never been demonstrated.

In predator-prey systems that have been characterized, predator aggregation most often occurs as a nonlinear (hyperbolic or sigmoidal) function of increasing prey density (Holling 1965, Murdoch & Oaten 1975). The sigmoidal (threshold) response is more common in higher vertebrates. In regard to behavioral and population ecology, it is also the most interesting response because it involves threshold-sensitive foraging behavior and tends to stabilize predator-prey systems (Hassell & May 1974, Steele 1974).

In a previous paper (Piatt et al. 1989), we described seasonal and annual (1982 to 1985) variations in the abundance and distribution of humpback, fin, and minke whales (*Megaptera novaeangliae*, *Balaenoptera physalus*, and *B. acutorostrata*) in relation to environmental conditions and the abundance of capelin *Mallotus villosus* in Witless Bay, Newfoundland, Canada. Humpbacks were the most common species observed on 214 days from both land-based and boat-based observation platforms, followed by minke and fin whales (10 : 3.5 : 1 ratio). Multiple regression analysis revealed that capelin abundance alone accounted for 63 % of the seasonal variation in total baleen whale abundance. The numbers of each whale species were strongly correlated with capelin abundance. Statistical analyses were performed on data grouped over 5 d intervals to reduce short-term variance, and to permit analysis of data from whale and capelin surveys that were not conducted on the same days.

In this paper we describe threshold foraging behavior of baleen whales in relation to the density of

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capelin schools in Witless Bay during the summers of 1983 to 1985. For this analysis, we use a subset of the above data in which hydroacoustic surveys for capelin and standardized watches for baleen whales were conducted on the same days (n = 61).

METHODS

In 1983 and 1984, whales were identified and counted during the course of 53 standardized hydroacoustic surveys for capelin in Witless Bay, using a 12 m vessel and following a ca 30 km transect line (for details see Piatt et al. 1989, Piatt 1990). Whale densities were calculated for each survey as the number of whales observed per h of survey effort. Data from 4 surveys in 1983 and 2 surveys in 1984 were excluded from analyses because of poor observation conditions (sea conditions ≥4 on the Beaufort scale). On 54 days in 1985, standarized 1 h whale watches were conducted during midday (11:00 to 13:00 h) from Gull Island in the middle of Witless Bay (Piatt et al. 1989). Hydroacoustic surveys (n = 29) for capelin (ranging between about 20 and 45 km in length) were conducted opportunistically from a charter vessel and were not standardized as in previous years. Whale observations were not recorded during these hydroacoustic surveys. Only those data for which both hydroacoustic and land-based whale surveys were conducted on the same days (n = 14) were used for analysis of whale foraging thresholds in 1985.

Echograms obtained from a Kelvin-Hughes Mark 2 echo sounder (1983 and 1984) or a Furuno Fishfinder (1985) were examined carefully for registrations of fish schools, and all individual schools were counted (Piatt 1987, 1990, Burger & Piatt 1990). Most capelin schools were located in the upper 20 m of the water column (Methven & Piatt 1991). Capelin school densities were calculated as the mean number of schools per linear km of survey. Based on the appearance of fish schools on echograms, fishery collections, and the diets of various predators, we concluded that virtually all pelagic fish registrations on echograms were due to capelin (Schneider & Piatt 1986, Piatt 1987, 1990, Schneider & Methven 1988, Methven & Piatt 1989, Burger & Piatt 1990).

A simple box model of a step-function was used to locate thresholds in plots of whale vs capelin density (Piatt 1987, 1990). The model used was:

$$W = k_1 C \text{ if } C > C_T;$$
$$W = k_2 C \text{ if } C < C_T,$$

where W = whale density; C = capelin school density; C_T = test threshold capelin density; and k_1 and k_2 = mean densities of whales above and below the test threshold C_T. Moving from intervals between the lowest observed capelin densities to the highest, the analysis is performed iteratively to generate a regression coefficient for each test threshold of capelin density. For a step (or sigmoid) function, r^2 increases with each iteration up to the threshold (inflection point), and decreases thereafter. The best fit to the step-function model occurs at the inflection point.

RESULTS

Hydroacoustic surveys indicated (Table 1) that capelin abundance in Witless Bay declined markedly between 1983 and 1984, and showed a moderate increase between 1984 and 1985. Observations on inshore capelin fisheries (Carscadden et al. 1987), and on the diets, abundance, and foraging time budgets of other capelin predators (Lear et al. 1986, Piatt 1987,

Table 1. Abundance of capelin schools and baleen whales observed on surveys in Witless Bay, 1983 to 1985. Note that survey methods in 1985 were different from those in 1983 to 1984 (see 'Methods')

	Year			Total
	1983	1984	1985	
No. of surveys	25	22	14	61
Mean (± SE) capelin abundance per survey (no. schools km^{-1})	7.2 ± 0.60	3.3 ± 0.66	5.3 ± 0.94	–
Mean (± SE) baleen whale abundance per survey (no. whales h^{-1})	1.1 ± 0.25	0.97 ± 0.41	2.1 ± 0.63	–
Estimated foraging threshold (no. capelin schools km^{-1})	7.3	5.0	5.8	–
Regression coefficient (r^2) at threshold[a]	0.66	0.78	0.91	–
Total no. of baleen whales:				
All whales	57	43	29	129
Humpback whale	49	23	21	93
Fin whale	3	2	0	5
Minke whale	5	18	8	31

[a] All regression coefficients significant at $p < 0.0001$ level

1990, Methven & Piatt 1989, 1991, Burger & Piatt 1990) corroborate our hydroacoustic data with regard to the relative scale and direction of changes in capelin abundance between these years.

Mean whale abundance changed little between 1983 and 1984, but increased between 1984 and 1985 (Table 1). However, mean values are somewhat misleading because whales were observed much less frequently in 1984, and were relatively abundant on the few days they were observed (Fig. 1). A frequency analysis is more revealing: sightings of ≥1 whale h^{-1} occurred on only 5 of 22 days (23 %) in 1984, in contrast to 12 of 25 days (48 %) in 1983, and 8 of 14 days (57 %) in 1985. Analysis of a larger dataset of whales (n = 394) observed h^{-1} from land-based surveys in 1983 to 1985 (Piatt et al. 1989) also revealed a dramatic change between years in humpback (1.04, 0.55, 2.11 whales h^{-1}, respectively) and minke (0.16, 0.35, 0.81 whales h^{-1}) whale abundance.

Plots of whale vs capelin abundance in each year (Fig. 1) reveal that baleen whales did not aggregate in Witless Bay until capelin school abundance exceeded threshold levels. Whales were observed on only 32 of the 61 days in which hydroacoustic surveys were conducted. The majority (96 %) of whales were observed only when local capelin school abundance exceeded 5.0 schools km^{-1} (which corresponds to ca 23 t km^{-2} in the study area; Piatt et al. 1989, Piatt 1990). The mean density of capelin schools on 61 different days ranged between 0.0 and 14.0 schools km^{-1} during the 3 yr of study.

The iterative step-function analysis revealed that thresholds in baleen whale responses to capelin school density in 1983, 1984, and 1985 occurred at capelin densities of 7.3, 5.0, and 5.8 schools km^{-1}, respectively (Figs. 1 & 2, Table 1). Using the step-function model and these thresholds, capelin density explained 66 to 91 % of the variance in baleen whale abundance (Table 1) – an improvement on the 63 % of variance explained by linear modelling in a previous analysis (Piatt et al. 1989). In contrast to the trend in mean whale abundance, foraging thresholds varied in accord with annual variations in overall capelin school abundance in the study area (Table 1).

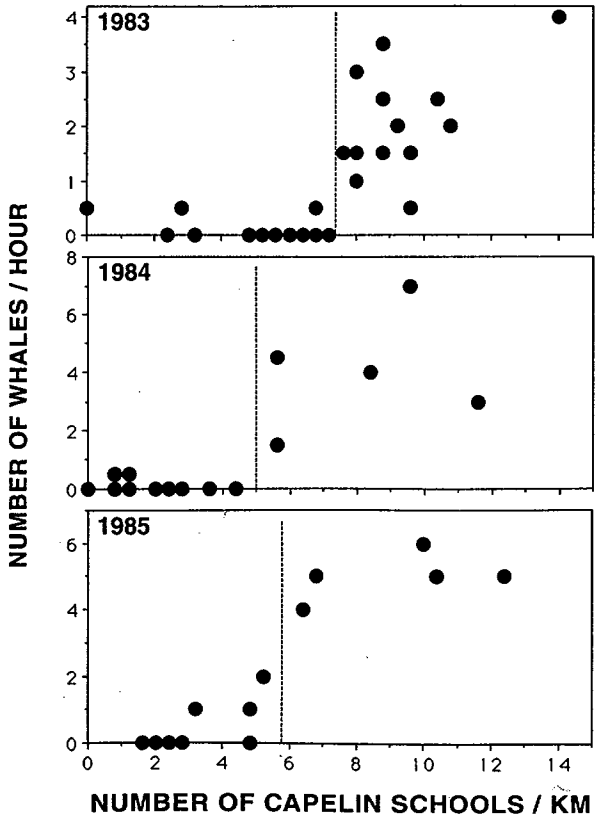

Fig. 1. Aggregation of baleen whales in Witless Bay as a function of local capelin school abundance. Indicated thresholds (vertical dashed lines) were estimated by iterative step-function analysis (see Fig. 2). Note that 7 and 1 duplicate observations are hidden (below thresholds) in plots of 1984 and 1985 data, respectively

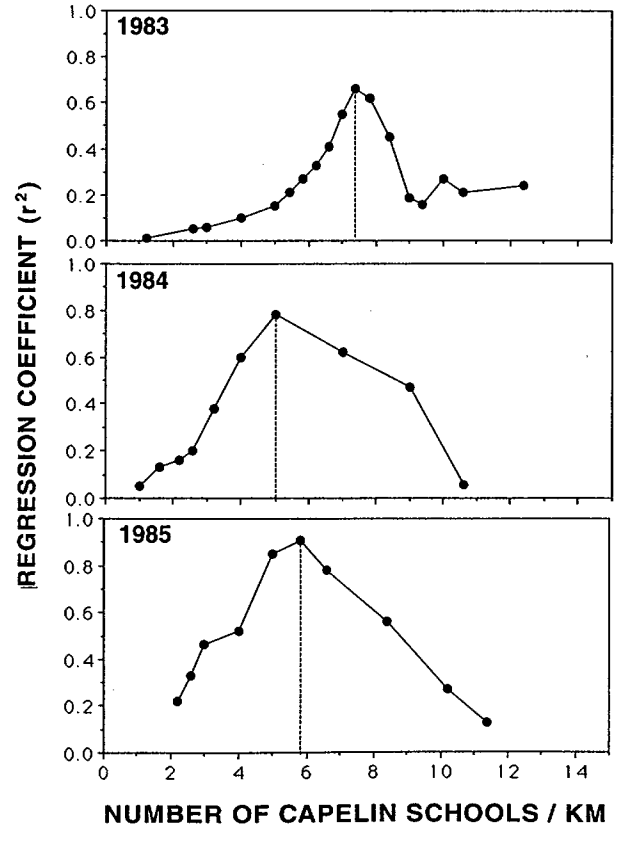

Fig. 2. Results of iterative step-function analysis. Regression coefficients calculated at each test threshold between observed values of whale abundance (Fig. 1). Best estimate of the actual inflection point (thresholds in Fig. 1) is indicated by the maximum r^2 value and marked by vertical dashed lines. See 'Methods' for details

DISCUSSION

The threshold foraging behavior exhibited by baleen whales in this study was predicted from body size considerations (Brodie et al. 1978, Kenney et al. 1986) and is consistent with other studies of predation behavior. Concurrent (1982 to 1984) studies of common murres *Uria aalge* and Atlantic puffins *Fratercula arctica* at Witless Bay showed that these capelin predators also exhibit threshold foraging behavior (Piatt 1987, 1990). Similar thresholds have been demonstrated for murres foraging on capelin in the Barents Sea (Erikstad et al. 1990). All vertebrate predators examined to date have exhibited non-linear aggregation behavior, and threshold foraging behavior is typical of higher vertebrates – particularly those that feed on highly aggregated prey like capelin (Holling 1959, 1965, Goss-Custard 1970, 1977, Hassel & May 1974, Murdoch & Oaten 1975). To our knowledge, however, this study provides the first documentation of threshold foraging behavior in marine mammals.

The foraging thresholds of baleen whales varied between years in relation to the overall abundance of capelin in Witless Bay. Similarly, murres and puffins at Witless Bay adjusted their foraging thresholds between days and years in response to seasonal and annual variations in local capelin abundance (Piatt 1987, 1990). This behavior is well simulated in 'Foraging by Expectation' models which assume that predators should change their expectations and foraging thresholds as prey density fluctuates (Green 1980, Iwasa et al. 1981). Although thresholds appear to be flexible over some range of medium to high prey densities, there is a lower limit of prey density below which foraging is unprofitable and aggregation does not occur. This limit is set by metabolic demands determined primarily by body size and to a lesser degree by foraging style (Nagy et al. 1984, Goudie & Piatt 1991). This probably explains why common murres, which are about twice the size of puffins but have a similar foraging style, foraged on significantly higher density schools of capelin than those used by puffins (Piatt 1987, 1990).

The prediction that baleen whales require high density prey aggregations to satisfy metabolic demands can be extended to hypothesize that large baleen whales should forage on higher density prey aggregations than small baleen whales. Thus, fin whales (ca 50 t) should forage on higher densities of prey than humpback (ca 33 t) and minke whales (ca 9 t, average adult masses from Whitehead 1981). Our data were insufficient to model threshold responses for each species separately owing to the relatively low frequency of minke and fin whale observations. However, our limited observations and those from other studies support the hypothesis that thresholds are related to body size:

(1) We observed fin whales only during peak summer periods of capelin abundance in Witless Bay (see Piatt et al. 1989). For the subset of that data used in this study, fins were observed when capelin densities were 8.8 and 9.2 schools km^{-1} on 2 days in 1983, and when capelin density was 9.6 schools km^{-1} on 1 day in 1984. Whitehead & Carlson (1988) and Watkins & Schevill (1979) also noted that fin whales prefer to forage on larger, denser prey aggregations than humpback whales.

(2) Minke whales were proportionately more abundant when capelin densities were low (minke/humpback ratio was 0.10, 0.78, and 0.38 compared to mean capelin densities of 7.2, 3.3, and 5.3 schools km^{-1} in 1983, 1984, and 1985, respectively). This suggests that minkes were more capable of exploiting low density capelin aggregations than humpback whales.

(3) Whale grouping behavior may reflect prey density requirements. The tendency for fins to form larger, more stable groups than humpbacks, as well as the tendency for minkes to forage alone, has been well-established (Perkins & Whitehead 1977, Watkins & Schevill 1979, Leatherwood et al. 1982, Edds & MacFarlane 1987, Whitehead & Carlson 1988). It may be that fins, and to a lesser degree humpbacks, coordinate their foraging attacks on prey schools to minimize prey dispersion and maintain high school densities (Whitehead 1983, Whitehead & Carlson 1988). Alternatively, high density prey patches are less common than low density patches, and predators that forage on high density prey must aggregate into fewer, more crowded sites (Atkinson & Shorrocks 1981, Piatt 1990). Regardless of whether whales group deliberately to concentrate their prey, or group incidentally at rare high-density prey patches, it appears that whale group size reflects the degree of prey aggregation required for successful foraging.

Whereas the hypothesis that body size and thresholds are correlated may be generally true in the *Balaenoptera*, it seems likely that morphological and behavioral adaptations would modify the absolute prey density requirements of other Mysticetes. For example, humpbacks have wider jaws and a greater filtering volume for their size than fin and minke whales, which have filtering volumes more closely scaled to their sizes (Lockyer 1976). Thus, humpbacks may be able to subsist on lower density prey aggregations than might be predicted on the basis of size alone. Slow-moving right whales *Eubalaena glacialis* skim prey near the sea surface and gray whales *Eschrichtius robutus* scrape prey off the sea bottom, and these divergent behaviors undoubtedly have an

influence on metabolic demands and hence prey density requirements. The quality and type of prey consumed (e.g. pelagic fish, euphausiids, benthic amphipods) is likely another source of variation among species. The degree to which these factors would influence metabolic rates and foraging thresholds is unknown.

Threshold foraging is a behavioral phenomenon with important ecological consequences. The rate at which predator populations change in response to fluctuations in prey populations is intimately linked to foraging behavior –which can vary markedly among species that share the same food resources (Holling 1959, 1965, Beddington et al. 1976, Rothschild 1991). Predation thresholds can provide stability in predator-prey systems in the absence of any other stabilizing mechanisms (Hassell & May 1974, Steele 1974, Murdoch & Oaten 1975). Foraging on different densities of shared prey also promotes the coexistence of species that share food resources (Steele 1974, Atkinson & Shorrocks 1981, Abrams 1983). With long-standing assertions of its fundamental importance in understanding marine community dynamics (e.g. Ivlev 1961, Steele 1974, Rothschild 1991), it is curious that we still know so little about the predation behavior of marine (and terrestrial) vertebrates. Given that we have drastically altered the populations of a multitude of higher marine vertebrates, this would seem a long overdue and potentially valuable topic for future research.

We have provided evidence to support the prediction that baleen whales require some minimum threshold level of prey density for successful foraging. Our prediction that different sized baleen whales should have different foraging thresholds can be tested rigorously with more directed surveys, and probably even with existing datasets (e.g. in the Antarctic where extensive surveys for krill have been conducted and 5 species of baleen whales are abundant). Whereas we could not do so with our simple hydroacoustic equipment, absolute prey density requirements (in no. or g m^{-3}) need to be more widely established so that marine ecologists and fisheries managers can better define the needs and functional relationships of fish, whales (e.g. Krieger & Wing 1986, Crawford & Jorgenson 1990), seabirds (e.g. Piatt et al. 1991), and other members of marine food webs.

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